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Density-dependent dispersal strategies in a cooperative breeder

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Abstract. Dispersal is a key ecological process that influences the dynamics of spatially and socially structured populations and consists of three stages—emigration, transience, and settlement—and each stage is influenced by different social, individual, and environmental factors. Despite our appreciation of the complexity of the process, we lack a firm empirical understanding of the mechanisms underlying the different stages. Here, using data from 65 GPS-collared dispersing female coalitions of the cooperatively breeding meerkat (*Suricata suricatta*), we present a comprehensive analysis of the effects of population density, mate availability, dispersing coalition size, and individual factors on each of the three stages of dispersal in a wild population. We expected a positive effect of density on dispersal due to increased kin competition at high densities. We further anticipated positive effects of mate availability, coalition size, and body condition on dispersal success. We observed increasing daily emigration and settlement probabilities at high population densities. In addition, we found that emigration and settlement probabilities also increased at low densities and were lowest at medium densities. Daily emigration and settlement probabilities increased with increasing female coalition size and in the presence of unrelated males. Furthermore, the time individuals spent in the transient stage increased with population density, whereas coalition size and presence of unrelated males decreased dispersal distance. The observed nonlinear relationship between dispersal and population density is likely due to limited benefits of cooperation at low population densities and increased kin competition at high densities. Our study provides empirical validation for the theoretical predictions that population density is an important factor driving the evolution of delayed dispersal and philopatry in cooperative breeders.

Key words: delayed dispersal; dispersal stage; distance; emigration; kin competition; meerkat; nonlinear dispersal; population density; settlement; transience.

Introduction

Dispersal of individuals is an important process regulating the persistence of populations as these populations depend on individuals that leave their natal patch, find suitable breeding habitat, and reproduce (Bowler and Benton 2005). Dispersal is typically divided into three stages: emigration from the natal group, transience through unfamiliar landscape, and settlement in a suitable habitat, and the outcome of a dispersal event depends on the decisions that dispersers take at each stage (Bowler and Benton 2005, Clobert et al. 2009). Nonetheless, existing theory often makes oversimplifying assumptions about dispersal and does not account for all three stages. Empirical data are particularly scarce for the transient and settlement stages due to the difficulty of following wide-ranging individuals under natural conditions (Tomkiewicz et al. 2010). In recent years, technological progress in animal tracking has allowed systematic collection of dispersal data (Cant et al. 2005, Schick et al. 2008, Singh et al. 2012), and advanced spatially explicit models have revealed previously unknown processes (del Delgado et al. 2010, Rémy et al. 2011, Debeffe et al. 2012, Tarwater and Beissinger 2012, Travis et al. 2012). However, our current knowledge of dispersal does not entirely capture the overall complexity, and more comprehensive empirical investigations of underlying mechanisms are needed (Bowler and Benton 2005, Clobert et al. 2009).

Among others, population density, resource availability and inbreeding avoidance have been proposed to influence dispersal of individuals and the transitioning between dispersal stages (Bonte et al. 2012, Travis et al. 2012). Population density can have positive or negative effects on the rate of emigration depending on several circumstances (Bowler and Benton 2005, Matthysen 2005). For instance, high densities in the natal area can reduce fitness due to increased resource competition and aggression among conspecifics (Bowler and Benton 2005), leading to a positive relationship between population density and emigration. At the opposite end, negative density-dependent dispersal can arise when high density is associated with high-quality habitat at the natal patch (Baguette et al. 2011) or when resources are unevenly distributed across space (McPeek and Holt 1992). Finally, a nonlinear relationship between population density and dispersal is expected where individuals emigrate at low population densities to avoid Alee effects (e.g., inbreeding, lack of breeding partners), remain in the natal area when densities increase and mates become more abundant, and disperse at very high densities when competition for resources intensifies (Courchamp et al. 1999, Loe et al. 2009, Shaw and Kokko 2014).

Density-mediated dispersal in social species is characterized by an additional level of complexity due to cooperation among group members. In these species, emigration can be negatively density dependent (Kokko and Lundberg 2001, Matthysen 2005) if the benefit of group living exceeds the cost

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of kin competition (Clutton-Brock 2002). At very low population densities, the benefits of cooperation decrease and individuals are more likely to disperse (Clutton-Brock and Lukas 2012, Hoogland 2013). However, this relationship is not always clear as competition at the natal site can decrease the inclusive fitness among kin (Hamilton and May 1977). Kin competition is, therefore, predicted to induce dispersal and several empirical studies support this prediction (Moore et al. 2006, Cote et al. 2007). In cases where kin competition outweighs the benefits of cooperation, population density is expected to have a positive effect on emigration. During transience, population density often has a negative effect on dispersal as saturated habitats increase the probability of aggressive encounters with conspecifics and decrease the likelihood of finding vacant territory (Kokko and Lundberg 2001, Lambin et al. 2001, Morton et al. 2018).

Several other intrinsic and extrinsic factors can be expected to influence the fate of a dispersal event. Larger individuals or individuals in better condition often have an advantage during transience and dispersal distance often increases with body mass (Barbraud et al. 2003, Jenkins et al. 2007, del Delgado et al. 2010, Debeffe et al. 2012). Individuals may move outside the range where relatives are found to avoid inbreeding (Long et al. 2008, Nelson-Flower et al. 2012), and the decision to settle in new territory is likely to be affected by the distribution of unrelated mates (Davidian et al. 2016). Social species may be able to overcome ecological constraints during dispersal by forming multiple-member dispersing coalitions (Brown et al. 1982, Courchamp et al. 2000, Clutton-Brock et al. 2001). Individuals in larger coalitions are predicted to experience reduced predation risk (Clutton-Brock et al. 1999, Courchamp et al. 2000) and have increased competitive ability (Packer et al. 1990, Wilson et al. 2002, Young 2004). Environmental factors can further affect dispersal patterns. For instance, low rainfall has been suggested to promote delayed dispersal as poorer body condition can inhibit dispersal and independent reproduction (Molteno and Bennett 2006).

Meerkats (*Suricata suricatta*) are cooperative breeders and thus well suited to simultaneously investigate the effects of social, individual, and environmental factors on dispersal. Meerkats live in groups of 2–50 individuals, and groups are characterized by the presence of a dominant pair that monopolizes reproduction (Clutton-Brock et al. 2008). During her pregnancy, the dominant female often evicts one or multiple subordinate females (Young et al. 2006). Spontaneous female emigration is not observed, and eviction is the main mechanism promoting dispersal (Clutton-Brock et al. 1998a). Age, body mass, and pregnancy status of subordinates promote their eviction (Clutton-Brock et al. 2008, Ozgul et al. 2014), and when two or more females are evicted simultaneously, they form same-sex multiple-member coalitions (Clutton-Brock et al. 1998a). Hereafter, we will use the term "dispersing unit" to indicate both multiple-member coalitions and individuals that disperse alone. After eviction, females remain within the territory of the natal group for a variable period (hereafter, referred to as "post-eviction phase"; Fig. 1). At the end of this period, they are either accepted back to the natal group (hereafter, referred to as "returners"), or permanently emigrate and enter transience (hereafter, referred to as "emigrants"; Fig. 1). Previous work has shown a positive relationship between emigration and natal group size (Ozgul et al. 2014) and we therefore expect density to play a key role throughout dispersal.

The aim of this study was to investigate how social (population density, mate availability, size of dispersing unit), individual (age, body mass, pregnancy status), and environmental (rainfall) factors influence the three stages of dispersal in female meerkats. For this purpose, we monitored 65 dispersing units throughout the entire dispersal process. Specifically, we expected (1) a positive relationship between population density and daily emigration rates, (2) a negative effect of density on dispersal distance and time to settlement, and (3) association with unrelated males, dispersing unit size, and pregnancy status of dispersers to interact with density.

Methods

Our study was conducted between September 2013 and March 2017 at the Kalahari Meerkat Project (KMP) located on the Kuruman River Reserve (26°59′ S, 21°50′ E), South Africa. The region is characterized by low seasonal rainfalls between October and April and large daily and seasonal temperature variations (Clutton-Brock et al. 1998b). Temperature and precipitation data were available from on-site weather stations.

GPS data collection

We fit lightweight GPS radio-collars (<25 g, ~3.5% of meerkat body mass) to subordinate females a few days prior to, or immediately after, eviction from the natal group. The collars were composed of a VHF module (Holohil Systems, Carp, Ontario, Canada) and a GPS module (CDD, Athens, Greece). To mount the collars, individuals were sedated using a mixture of isoflurane and oxygen in compliance with the KMP protocol (Jordan et al. 2007). All necessary permits to handle and tag meerkats were granted to the KMP by the Department of Environment and Nature Conservation of South Africa and the Animal Ethics Committee of the University of Pretoria (permit "FAUNA 192/2014"). We used GPS locations to identify time of emigration and time of settlement, and to calculate dispersal distance and elapsed time between emigration and settlement. We distinguished emigration and settlement based on visual investigation of the inflection points of the net squared displacement (NSD) plots (Cozzi et al. 2016). The NSD measures the square of the Euclidean distance from the place of eviction to any given GPS location along the dispersal path (Börger and Fryxell 2012). We further used field observations to validate the times of emigration and settlement identified by the NSD approach (see Appendix S1 for more details).

Field data collection

We located dispersing units by means of VHF radio-tracking every two to seven days. At each visit, we recorded data on dispersing unit size, number of associated unrelated males, pregnancy status, and body mass. Study animals were part of a long-term research project, habituated to the presence of people, and trained to climb onto a portable weighing scale (Clutton-Brock et al. 1998b). Over the study

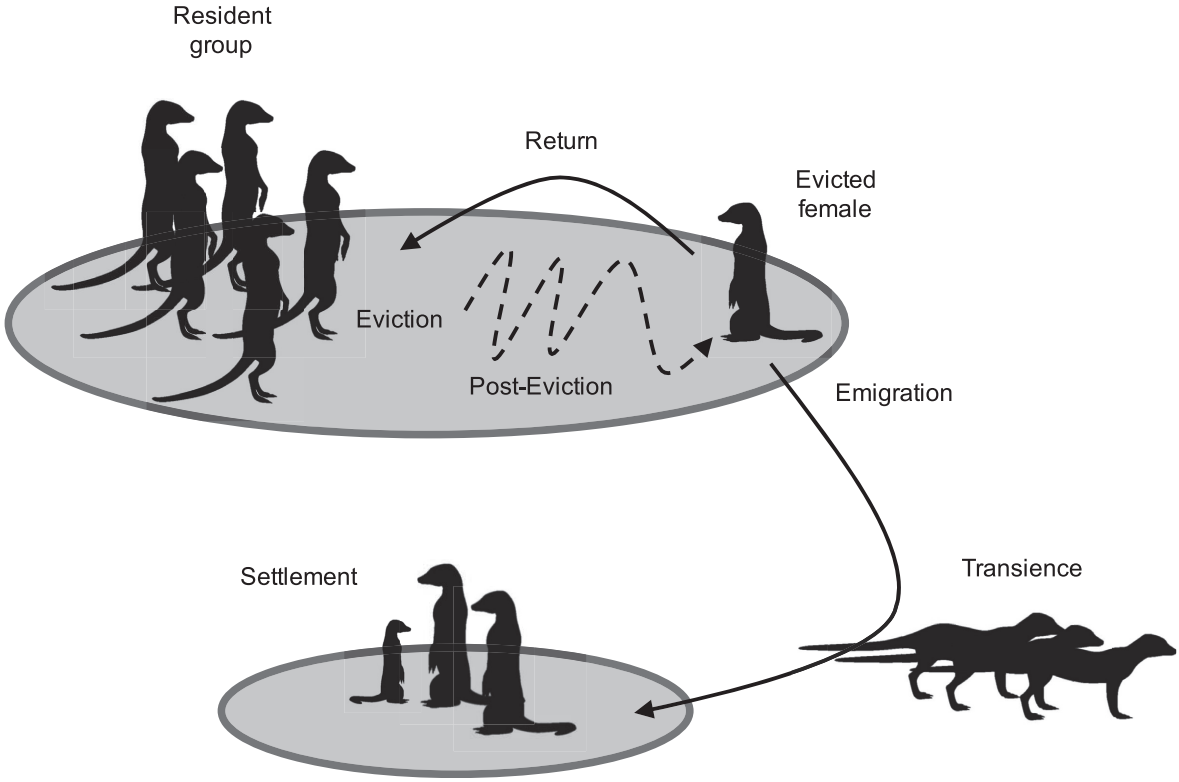

FIG. 1. Schematic representation of female meerkat dispersal. During pregnancy, a dominant female typically evicts one or several subordinate females from the natal group. Evicted females remain in the natal territory (large gray circle) for a variable period (post-eviction phase). At the end of the post-eviction phase, females return to the natal group or emigrate from the natal territory. Returners help to raise the offspring of the dominant female and emigrants enter transience, settle in new territory (small gray circle), and breed.

period, we monitored a total of 65 female dispersing units. Dispersing units, i.e., any single female or group of related females evicted from the natal group, ranged from 1 to 6 females. Dispersing individuals were between 9 months and 5 yr of age at the time of eviction.

Population density calculations

Virtually all resident meerkat groups within the study area were known and censused during the study period. To estimate population density (individuals/km^2), we divided the number of all known resident individuals (i.e., total population size) by the size of the study area. Resident groups were visited by volunteers several times each week as part of the long-term activities at the KMP. At each visit, volunteers collected information on group composition and recorded GPS locations with handheld GPS devices (Garmin, Olathe, Kansas, United States). We defined the size of the study area as the combination of 95% kernel home ranges of all resident groups (Calenge 2006). A detailed description of the methods and smoothing parameter estimators can be found in Cozzi et al. (2018). All parameter calculations and statistical analyses were done in R (R Core Team 2013).

Statistical modeling

All analyses described here (1–4) were carried out at the dispersing unit level. We quantified the effects of social, individual, and environmental factors on (1) daily emigration probability, (2) daily return probability, and (4) daily settlement probability using three separate Cox proportional hazard models with mixed effects implemented in the function coxme of the R library coxme (Therneau 2018). The hazard rate $h[t]$, which in our case indicates the likelihood of transitioning from one stage to the next (e.g., transience to settlement) for a given time step, was calculated at daily intervals. We used time-dependent covariates where each day t appears as a separate observation. To investigate (3) transience, we quantified the effects of the same factors on dispersal distance and dispersal time with two separate linear models using the function lm in R. In all four analyses (Cox proportional hazard and linear models), we used model selection to test all combinations of predictor variables. Model selection was based on Akaike's Information Criterion (AIC) and performed using the library MuMin (Bartoń 2018). Details for full models, outcomes of model selections, and descriptions of how we accounted for colinearity and temporal autocorrelation are given in the Appendices S2–S6.

Emigration

To investigate the daily emigration probability of dispersing units we only used units that emigrated from the natal territory. Units that died or were lost from the study before emigration were right censored (Fox and Weisberg 2011).

We included *mass* and *age* of the oldest dispersing unit member, population density (pop) and its squared value (pop^2) to account for nonlinearity, rainfall (rain), the number of females in a dispersing unit (female), whether or not males were present (male), pregnancy status of unit members (preg), as well as the pregnancy status of the dominant female at the natal group (pregnatal), and biological meaningful interactions. We used the random terms year, the year in which a unit dispersed, and origin, the natal group identity from which a unit originated. Further details on model parameters can be found in the Appendix S2.

Return

To investigate the daily return probability of dispersing units, we only used dispersing units that returned to their natal group (Appendix S3). Units that died or were lost were right-censored. We included the same explanatory variables used in the Emigration model: mass, age, pop, pop^2, rain, female, male, preg, and pregnatal. We fitted the random terms year and origin.

Transience

Distance.—We investigated the Euclidean dispersal distance between the emigration location and the location at settlement (Appendix S4). For this model and the Time model described in the next subsection, we only considered dispersing units that emigrated from their natal territory and settled in a new territory. We square-root transformed the response variable dist to meet assumptions of normality. We included mass and age at the time of emigration, and pop, pop^2, and rain at the time of settlement. We further included the association with males at the time of emigration (male) and the dispersing unit size (unit) at the time of settlement. Here, sample size was small because we included only dispersing units that emigrated, and we did not include random effects to avoid overfitting of the model. However, we tested for repeatability of measures across years (Stoffel et al. 2017) and did not detect repeatability.

Time.—We investigated the number of days elapsed between emigration and settlement (Appendix S5). The response variable *time* followed a square-root-normal distribution and was therefore square-root-transformed. We fitted the same explanatory variables used in the model Distance: mass, age, pop, pop^2, rain, unit, male. We performed this model on the same data set as the Distance model and did not include random effects (see explanation above).

Settlement

To investigate the settlement probability of dispersing units we only used dispersing units that emigrated from their natal territory (Appendix S6). Units that died or were lost were right-censored. The difference between this model and the models Emigration and Return is that time t represents the number of elapsed days since emigration and not since eviction. We included the following explanatory variables: mass, age, pop, pop^2, rain, female, male, and preg. We used the random terms year and origin.

Results

Females were evicted from their natal groups either alone or as several females at a time, forming same-sex dispersing units that varied in size from one to six related females. Thirty-four of the 65 evicted dispersing units (52%) returned to their natal groups, after an average post-eviction phase of 26.4 d (interquartile range: 9–35 d). Twenty-six units (40%) emigrated from their natal territory, after an average post-eviction phase of 26.0 d (9–37 d). Three units died and two units were lost after eviction. Of the 26 units that emigrated, 18 units settled in a new territory after an average transience of 38.8 d (13–59 d), one died, three were lost, one joined another unit, and three returned to their natal group.

Due to very low rainfall during the wet season between October 2015 and April 2016, the population size dropped below 50% of the size observed at the start of the study, in September 2013. This produced a gradient in population density that varied between 1.7 and 4.2 individuals per km^2 during the 3.5-yr study period and offered an opportunity to study the effects of population density on each stage of female meerkat dispersal in a relatively short time frame. In Fig. 2A, we divided densities in three equal bins with similar sample size: low (1.7–2.8 individuals/km^2, $n = 168$), medium (2.8–3.5 individuals/km^2, $n = 239$), and high (3.5–4.2 individuals/km^2, $n = 220$) population densities.

Emigration

Daily rates of emigration varied with population density. We observed a nonlinear relationship between population density and emigration (Exponential coefficient $\beta = 30.56$, Estimate = 3.42, SE = 2.12, Appendix S2). Daily emigration probability was highest at low population density, lowest at medium densities and high again at high densities (Fig. 2A). After eviction, large dispersing units emigrated earlier from the natal territory than small units (Fig. 2A), and this effect was most pronounced at medium densities ($\beta = 0.41$, Est = −0.89, SE = 0.36). The presence of unrelated males increased the daily emigration probability of female dispersing units ($\beta = 3.45$, Est = 1.24, SE = 0.62), and this effect was stronger in large female units ($\beta = 7.06$, Est = 1.95, SE = 0.77, Fig. 2B). Amount of rain during the previous nine months decreased the daily probability of emigration ($\beta = 0.65$, Est = −0.43, SE = 0.22). Body mass of the oldest unit member, age of oldest unit member, and pregnancy status of the dominant female at the natal group did not influence daily emigration probability.

Return

Population density increased the daily probability that evicted units returned to their natal groups ($\beta = 2.27$, Est = 0.82, SE = 0.30). Such probability decreased with increasing age of the oldest unit member ($\beta = 0.44$, Est = −0.82, SE = 0.26), and when one or more females in the unit were pregnant ($\beta = 0.51$, Est = −0.68, SE = 0.45, Fig. 3A). When the dominant female in the dispersing unit's respective natal group was pregnant, return time to the natal group increased ($\beta = 0.28$, Est = −1.26, SE = 0.42). Return to the natal group was associated with increased rates of

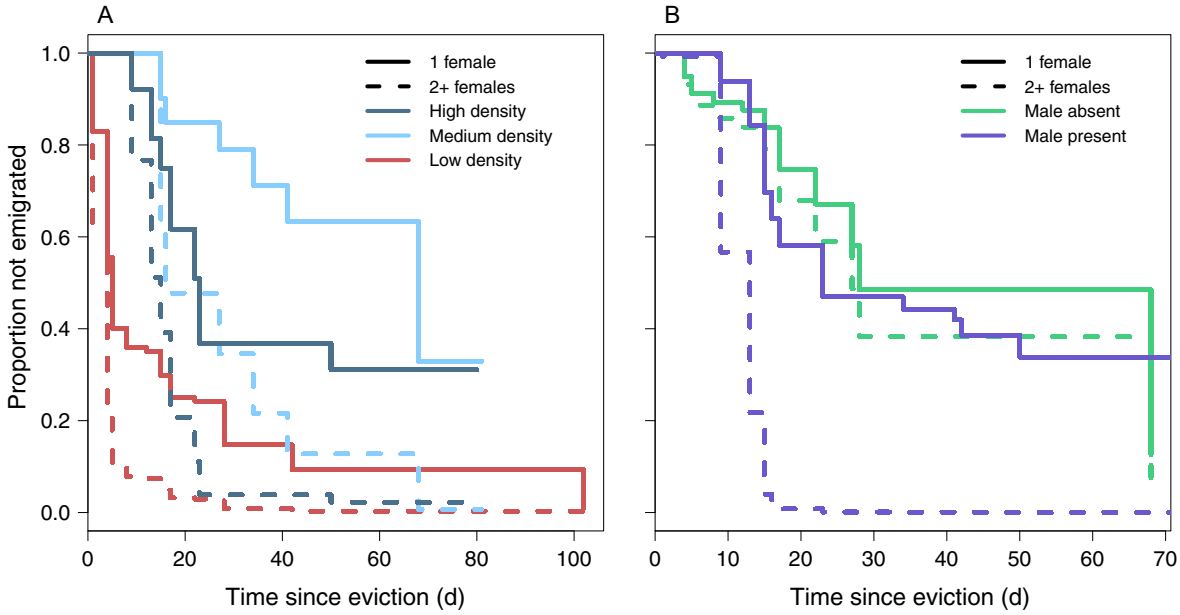

FIG. 2. (A) Kaplan-Meier plot showing the effect of number of female meerkats (single evicted female, 1; two or more females grouped together in a coalition, 2+) on daily emigration probability at low (red), medium (light blue), and high population densities (dark blue). (B) Kaplan-Meier plot showing the effect of number of female meerkats on daily emigration rate in the absence (green) or presence of unrelated males (purple).

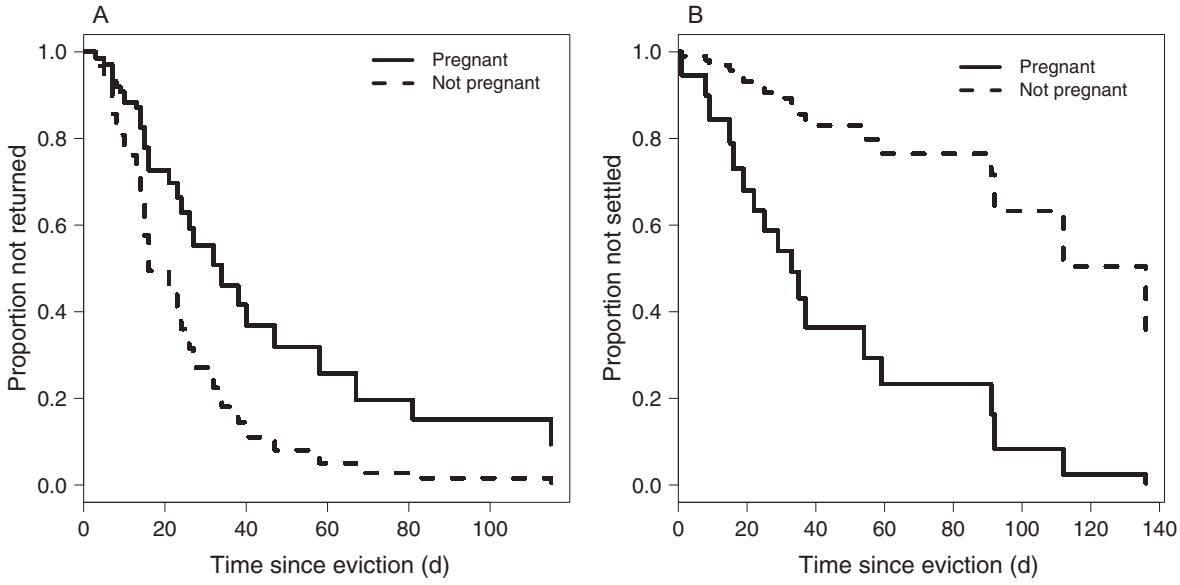

FIG. 3. (A) Kaplan-Meier plot showing the effect of pregnancy (at least one female in the dispersing coalition is pregnant) on daily return probability of evicted female meerkats, including only those that returned to their natal group (34 out 65 coalitions). (B) Kaplan-Meier plot showing the effect of meerkat pregnancies on daily settlement probability.

abortion in pregnant dispersing females. Sixty-two percent of pregnant dispersers aborted their litters before being accepted back in the natal group. Of the 38% of the successfully born litters, only 42% survived to the first month (Appendix S7). Rain during the previous nine months decreased the daily probability to return ($\beta = 0.45$, Est = −0.81, SE = 0.27). Body mass of the oldest unit member, unit size, and presence of males did not influence daily return probability of dispersing units.

Transience

Distance.—The average straight-line dispersal distance between emigration and settlement was 2.24 km (interquartile range: 1.08–2.66 km), and it was negatively correlated with dispersing unit size (Est = −7.45, SE = 1.63, Fig. 4A). Females that had grouped with males during the post-eviction phase settled closer to the natal territory than females that had not found males during this period (Est = −19.65,

SE = 5.52, Fig. 4A). Rain in the nine months prior to settlement had a small negative effect on dispersal distance (Est = −0.14, SE = 0.05). Population density and body mass and age of the oldest unit members did not influence dispersal distance.

Time.—Dispersing units spent an average of 46 d (interquartile range 16–57 d) in transience before they settled. Population density was the only factor that influenced time to settlement. When population density was high, dispersing units spent more time until they settled (Est = 2.11, SE = 1.15, Fig. 4B). Rainfall, body mass, and age did not influence dispersal time.

Settlement

Daily rates of settlement varied with population density. During settlement, population density and rainfall were correlated; we therefore fitted two models to account for both variables separately: one including population density, but not rainfall (Appendix S6, Table S1a); and one including rainfall, but not population density (Appendix S6: Table S1b). The relationship between population density and daily settlement was not linear (β = 34,708.01, Est = 10.45, SE = 7.81, Appendix S6: Table S1a). Daily settlement probability was high at low population densities, low at medium densities, and high again at high densities (Appendix S6: Table S1a). Large dispersing units settled earlier than small units (β = 9.14, Est = 2.21, SE = 0.70, Appendix S6: Table S1a). The presence of unrelated males increased overall daily settlement probability (β = 27.18, Est = 3.30, SE = 1.86, Appendix S6: Table S1b), but this effect was weaker the more females were present in a dispersing unit (β = 0.15, Est = −1.87, SE = 1.80). Pregnancies increased the daily settlement probability of dispersing units (β = 2,106.94, Est = 7.65, SE = 3.81, Fig. 3B). As opposed to females that returned to the natal group, females in dispersing units that emigrated successfully carried through 89% of their pregnancies, of which they only lost 35% within the first month (Appendix S7). Rain during the previous nine months decreased the daily probability of settlement (β = 0.33, Est = −1.10, SE = 0.59). Body mass and age of the oldest unit members did not affect daily settlement probability.

Discussion

Our study showed that interactions between social, individual, and environmental factors affected each of the three dispersal stages differently. Further, our findings emphasize the central role of population density on dispersal. We found that daily emigration probabilities were high at low and high population densities, and lowest at medium densities, suggesting a nonlinear relationship. Increasing population density also resulted in increased time spent in the transient stage. The size of the dispersing unit had a positive effect on daily emigration and settlement probabilities, and large units emigrated earlier than small units. We further showed that dispersal distance decreased with increasing numbers of females present in a dispersing unit and when unrelated males were present. These social factors were more important drivers of dispersal than individual characteristics such as body mass and age of the oldest unit member, with the latter only influencing daily return probabilities of dispersers.

Our findings are consistent with the theoretical predictions that the limited benefits of cooperation at low population density can enhance emigration rate in social species

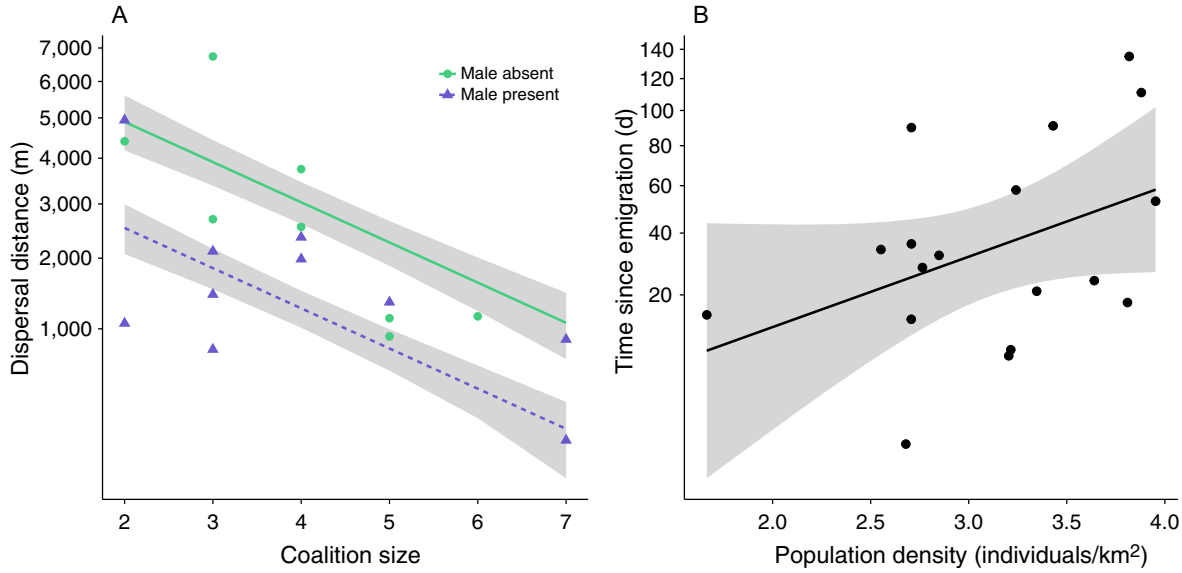

Fig. 4. (A) Effect of mean meerkat coalition size (females and unrelated males) on net displacement (square-root transformed) between place of eviction and place of settlement. Female meerkats that did not group with males during post-eviction are shown in green, females that grouped with males during post-eviction are shown in purple. (B) Effect of population density (individuals per km^2) on female meerkats' dispersal time between emigration and settlement (in days, log transformed). Lines show predicted values and gray shaded areas show 95% confidence intervals.

(Hoogland 2013), and that at moderate densities, where the benefits of cooperation are expected to increase and exceed the costs of kin competition, individuals are more likely to remain in the natal patch (Clutton-Brock 2002, Matthysen 2005). Finally, the increased emigration rate at high densities may be best explained by increasing costs of kin competition that exceed the benefits of cooperation (Cote et al. 2007). A similar nonlinear relationship has been proposed in other systems (Kim et al. 2009, Rousset 2012). The negative relationship between population density and emigration at low population size suggests that meerkats are subject to an Allee effect, i.e., inverse density dependence at low density (Allee et al. 1949), which can be caused by different factors such as inbreeding, demographic stochasticity, or a reduction of cooperative interactions when fewer individuals are present (Courchamp et al. 1999). In the cooperatively breeding meerkat, inverse density dependence potentially decreased inclusive fitness and promoted emigration to escape the consequences of an Allee effect induced by reduced cooperation.

Our results showing negative density-dependent emigration, transience time, and settlement support the theoretical prediction that population density promotes the evolution of delayed dispersal and philopatry in cooperative breeders (Kokko and Lundberg 2001, Platt and Bever 2009). In many species, aggression from conspecifics is predicted to increase, and chances of finding vacant territory to decrease with increasing density (Lambin et al. 2001). Thus, staying at home and gaining inclusive fitness through cooperation can be an adaptive life-history strategy when vacancies are unavailable (Kokko and Lundberg 2001). In meerkats, this hypothesis is further supported by the fact that evicted females were more likely to return to the natal group at high population densities, and by previous findings, showing that dispersing meerkats avoided areas where conspecifics were found (Cozzi et al. 2018). We found higher emigration and settlement rates after periods with low rainfall. Our results therefore do not support the hypothesis that diminished body condition due to low rainfall promotes the evolution of delayed dispersal (Jarvis et al. 1994, Molteno and Bennett 2006). We suggest that the local depletion of resources caused by low rainfall increases competition over limited resources and forces individuals to leave their natal site (Greenwood 1980).

We observed an important effect of mate availability during different stages of the dispersal event. Those females that associated with unrelated males in the early stages of the dispersal event (i.e., post-eviction) were characterized by early emigration rate and reduced dispersal distance, while those who did not associate with unrelated males either delayed emigration or dispersed a considerable distance. Most of the males that joined females during post-eviction were from outside the study area (N. Maag, *personal observation*), suggesting that males traveled longer distances than females, who generally settled close to the natal territory (Fig. 4A). Male-biased dispersal and female philopatry is widespread in mammals and suggested to avoid inbreeding (Pusey 1987, Long et al. 2008). Females dispersed further if they did not associate with males during post-eviction, possibly to reduce the risk of inbreeding if no unrelated males were available at the onset of dispersal. Mate availability seems to be more important for the dispersal decision of meerkats than individual traits such as body mass, although the latter was shown to be important within and across other species (Jenkins et al. 2007, del Delgado et al. 2010, Debeffe et al. 2012, Stevens et al. 2014). Our findings are in line with a recent study showing that, in a social species, the distribution of breeding partners was more important for dispersal patterns than individual phenotypes (Davidian et al. 2016). However, to assess the influence of phenotypic traits on dispersal, an investigation at the individual level may be more informative.

Dispersing in large coalitions may reduce the costs of traveling away from the natal group and increase the competitive abilities of dispersers during transience and settlement (Bernasconi and Strassmann 1999, Boswell et al. 2001). After settlement, having several helpers present will likely increase reproductive success and improve group augmentation (Clutton-Brock et al. 1999, Kokko et al. 2001, Russell et al. 2002). Our results, showing that large dispersing coalitions had higher daily emigration and settlement probabilities than small coalitions and single females, are consistent with the assumption that increased coalition size is beneficial for dispersal in social species. Large coalitions emigrated earlier than small coalitions when population density was most restrictive (i.e., at medium densities, Fig. 2A), suggesting a competitive advantage with increasing coalition size. This is because aggression from conspecific residents increases at higher densities and larger coalitions are more likely to win aggressive encounters (Packer et al. 1990, Wilson et al. 2002, Young 2004). In addition, traveling with other individuals can reduce the costs (i.e., body mass, stress hormones, immune defense, survival) induced during extra-territorial forays or floating that often precede dispersal (Creel and Creel 2002, Young 2004, Ridley et al. 2008). Due to the difficulty of following dispersers, however, the effect of coalition size on body condition during the later stages of dispersal was never quantified and remains to be tested empirically.

In most cooperative species, a single dominant female monopolizes group reproduction (Koenig and Dickinson 2004, Clutton-Brock et al. 2010). However, subordinates occasionally breed thereby reducing the fitness of the dominant individual (Koenig and Dickinson 2004). Dominant individuals may therefore attack subordinates to induce chronic stress and reduce their fertility (Wingfield et al. 1991, Creel 2001). However, several studies have shown that dominant individuals had higher stress hormone levels than subordinates and suggested that reproductive suppression is not maintained through social stress (Abbott et al. 1997, Creel 2001). In meerkats, temporary evictions of subordinate females were previously shown to increase their stress levels and abortion rates (Young et al. 2006). Our results confirm Young et al. (2006) findings and provide further support for the stress-related suppression hypothesis. In addition, we provide new insight into the outcome of pregnancies when subordinates emigrate instead of return. The daily probability of settlement increased substantially if an emigrant female was pregnant (Fig. 3B), and emigrants mostly remained pregnant during transience and successfully gave birth after settlement (Appendix S7). Pregnant females may be forced to promptly find vacant territories for settlement in a shorter period so parturition can occur in

a permanent burrow, as a safe territory is crucial for offspring growth and survival (Bronson 1985, Clutton-Brock et al. 1989). Survival of the first litter may be crucial for fast group augmentation and successful group establishment, as offspring from the first litter will increase success of the following litters (Clutton-Brock et al. 2001).

In conclusion, we propose that both cooperation (at low numbers) and kin competition (at high numbers) are responsible for the nonlinear effect of population density on daily emigration and settlement rates of female meerkats (Platt and Bever 2009, Hoogland 2013). A nonlinear relationship between population density and dispersal can also occur in non-social species, although it may be caused by different factors such as low mate availability and resource competition (Loe et al. 2009, Rousset 2012). During transience and settlement, a negative association between population density and dispersal may be expected for various vertebrate species (Lambin et al. 2001, Wilson et al. 2017). Different species may, however, show different reactions to population density. For example, non-territorial species, such as marine birds, show a positive relationship between population density and settlement probability, because patches with high density correspond to areas of high resource abundance (Fernández-Chacón et al. 2013). Although we suggest that the negative association between meerkat dispersal and population density is due to a reduction in cooperation at home and increased chances of finding vacant territory (Kokko and Lundberg 2001, Platt and Bever 2009), alternative factors such as the spatial distribution of resources may play an important role (McPeek and Holt 1992, Baguette et al. 2011). Where resources are not uniformly distributed, for example when resources become abundant in a previously unoccupied, but now suitable habitat (e.g., invasion during range expansion), emigration rate may increase at lower densities (Travis et al. 2009). Future studies investigating the effect of social, individual, and environmental factors on all three stages of dispersal will improve our understanding of the effect of population density and other drivers on dispersal and consequently population dynamics.

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